reproducing the upperside, outlined with black proximally. Post discal spots well marked, as in *kilimensis*. Hindwing with black lines very narrow, thinly outlined in whitish. Post discal lunules more or less distinct, marginal lunules yellow, well defined.

Holotype male. TANZANIA: Mt. Oldeani, 20.iii.1973 (J. Kielland). Allotype female, same locality, 17.iii.1973 (J. Kielland). Both deposited in the B.M. (N.H.).

Paratypes. 11 ♂ ♂, eight ♀ ♀, in collections of J. Kielland, R. Henning, J. Plantrou, B. Turlin.

Range: Only known at present from the type locality.

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NOTES ON FLEAS (PART II): THE INTERNAL ORGANS: CAN THEY THROW ANY LIGHT ON RELATIONSHIPS WITHIN THE ORDER?*

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INTRODUCTION

It is curious that Rothschild and Jordan concentrated exclusively on the external anatomy and morphology of fleas and did not so much as glance at their internal organs: the fact was neither of them had time to do so. Rothschild was a banker with multiple responsibilities and varied activities, of which nature conservation was a major commitment (Hopkins & Rothschild, Vol. I, 1953). He found that collectitng and the study of mounted material filled his leisure hours** and vacations and also satisfied the requirements of the Plague Commission (Hirst, 1953, pp. 177-80). Nevertheless he had his assistant, Cox, trained as a section cutter in the Cambridge Department of Zoology, and invested in a Cambridge rocker, but only 15 serial sections seem to have been cut and saved for future reference. Jordan, until he became director of the Tring Museum in 1930 (seven years after his collaborator's death) also regarded fleas as a spare time hobby, although he once told me a little wistfully that both he and my father had originally planned to section their material as well as study whole mounts. As for my own investigations, these have always been in connection with circumscribed and specific problems. Thus, in order to establish the suspected link between the mammalian hormones and the reproductive cycle

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* Part of a lecture prepared for the July 1975 meeting of the British Entomological and Natural History Society. 'Notes on Fleas' in the Society's Vol. 2, part 1 (1969) was the first portion of this lecture.

** My mother once told me with amused affection that when my father reached home at 6 p.m. after a ten-hour day in the City, he would immediately peel off his jacket and say: 'Dearest, come and sit with me while I mount my fleas'. That was the sum total of the evening's amusement offered to his bride of a few months.

of the rabbit flea, it was necessary to examine their internal organs. Similarly when we inquired how fleas jumped, it was impossible to attempt an answer by gazing at their exoskeletons. Never at any time did I envisage, let alone attempt, a serious study of comparative morphology of the soft parts of the different families or genera of fleas*. Nevertheless it was

* The 32 species which were duly sliced up (Table 1) — and I certainly looked at no fewer than 600,000 sections in the process — present a most unbalanced crazy selection for any purpose other than the study of hormones and jumping activity.

TABLE I

Species of Fleas cut in Serial Sections

		No. sectioned
Pulicidae		
Ctenocephalides felis (Bouché)	♂ ♀ & pupa	25
Ctenocephalides arabicus (Jordan)	♀	2
Spilopsyllus cuniculi (Dale)	♂ ♀ & pupa	6,000
Cediopsylla simplex (Baker)	♂ ♀	25
Cediopsylla tepolita Barrera	♂ ♀	5
Hoplopsyllus pectinatus Barrera	♂ ♀	5
Archaeopsylla erinacei (Bouché)	♂ ♀	over 100
Echidnophaga gallinacea (Westwood)	♂ ♀	50
Tunga penetrans (Linnaeus)	♀	3
Tunga monositus Barnes & Radovsky	♂ ♀ & pupa	20
Tunga sp. near monositus (Traub's undescribed sibling species)	♀	3
Tunga caecigena Jordan & Rothschild	♀	1
Ancistropsyllidae		
Ancistropsylla nepalensis Lewis	♂ ♀	5
Ceratophyllidae		
Nosopsyllus fasciatus (Bosc)	♂ ♀ & pupa	over 100
Ceratophyllus gallinae (Schrank)	♂ ♀ & pupa	over 100
Ceratophyllus rusticus Wagner	♂ ♀	25
Dasypsyllus gallinulae (Dale)	♂ ♀	10
Ceratophyllus farreni Rothschild	♀	10
Nosopsyllus londiniensis (Rothschild)	♂ ♀	2
Pleochaetis 'melanotis'	♂ ♀	25
Hystrichopsyllidae		
Hystrichopsylla talpae (Curtis)	♂ ♀	50
Stenoponia tripectinata (Tiraboschi)	♂ ♀	15
Rhadinopsylla pentacantha (Rothschild)	♂ ♀	2
Ctenophthalmus nobilis (Rothschild)		5
Strepsylla sp.	♂ ♀	5
Rhopalopsyllidae		
Polygenis klagesi (Rothschild)	♂ ♀	5
Rhopalopsyllus australis tupinus Jordan & Rothschild	♂ ♀	5
Vermipsyllidae		
Chaetopsylla rothschildi Kohaut	♂ ♀	10
Stephanocircidae		
Craneopsylla minerva wolffheugeli (Rothschild)	♂ ♀	5
Ischnopsyllidae		
Ischnopsyllus octactenus (Kolenati)	♂ ♀ & pupa	10
Leptopsyllidae		
Stigmactenus toxopeusi Smit	♂ ♀	7
Pygiopsyllidae		
Papuapsylla luluai Holland	♂ ♀	5

impossible for anyone with a love of shapes and textures, and an appreciation of brilliant and fascinating stain-engendered colours, not to ask occasionally whether the insides of fleas threw any light on their phylogeny and relationship. Jordan and Rothschild, with their creative and intuitive interpretation of the exoskeleton and external morphology, had produced such a sound classification of fleas that they left us with virtually nothing but mopping up operations on our hands. Seen within this framework I think my own meagre observations on the soft parts of fleas upholds their arrangements and there is certainly plenty of support for Jordan's views (see Hopkins & Rothschild, Vol. III, 1962, p. 1) also recently confirmed by Smith (1972) that the Hystrichopsyllidae should be accorded the rank of a super family. It also underlines another observation of Jordan's, namely that it is almost impossible to classify these insects on a few major characters, but a combination of a certain number of the less obvious and unobtrusive features (not all of which, but a majority of which will be found in the same related species or group of related species) is required. Only occasionally is a single major character involved. Thus the Tunginae and Echidnophaginae are the only subfamilies of fleas with a reduced number of rectal papillae (see below), but in the great majority of cases we are dealing with a mass of minor variations imposed — as in the case of differences in the exoskeleton — on a curiously similar and rigid ground plan. These variations, when added to well selected characteristics of the exoskeleton, are nevertheless important. In the following notes I have not attempted a detailed comparison between major structures such as the aedeagus, or the female organs associated with copulation and fertilisation, or the proventriculus, or jumping apparatus, but have drawn attention to a few organs and other features of the internal anatomy which have hitherto received relatively little attention.

The fleas to be sectioned were fixed in Bouin Brazil for 24 hours at a temperature of 40°C, stained with a modified Mallory's triple stain and cut at 8 μm.

GENERAL CONSIDERATIONS

The internal organs of the flea, which cannot be seen from the outside, display the same order of variation between species as the external organs. Many of these differences are self evident and closely linked to the general morphology. Thus the shape of a flea's brain is different in a Helmet flea and in *Xenopsylla*. The compact body of Pulicid fleas results in a closely knit nerve cord, whereas, e.g. in many Pygiopsyllidae, the ganglia are well spaced out and the nerve cord appears to straggle (Figs. 1a & b). Other differences, which are not apparent from the outside, reflect the life style of the species, such as the size and secretions of the salivary glands.

Stained with a modified Mallory's triple stain, tanned cuticle appears amber yellow, brown and black (this is considered by Richards (1951) and Wigglesworth (1965) to be sclerotised and melanised exocuticle), untanned cuticle is pillar-box red (this is the mesocuticle of these authors) and endocuticle and arthrodial membrane stains butcher blue. Baker (1958) states that aniline blue is a large anion which can only penetrate the spaces between the molecular chains when these are relatively large; the denser structure of mesocuticle excludes it, but is permeated by the smaller acid fuchsin or azocarmine anion while neither can enter tanned exocuticle. Whitten (1972) states that cuticle may proceed through any or all of these stages in orderly sequence. Certainly in fleas there are many areas in which blue and red staining cuticle merge into each other (e.g. in laminated body

wall of the neosomic female of *Tunga*, and the male ejaculatory bulb of various species), but there are also areas where the junction is sharp. In the pharate adult all but a few specialised areas of the cuticle are as yet untanned, and hence stain pillar-box red.

In specimens mounted in Canada balsam, untanned cuticle and arthrodial membranes are virtually transparent and they are indistinguishable from each other. Thus in whole mounts the so-called lunar and satellite sclerites of the roof of the capsule (which are frequently used as taxonomic characters, Rothschild & Traub, 1971) are the well tanned (and therefore clearly visible) portions of a much larger area of untanned (virtually invisible) cuticle. Such an arrangement results in some portions of the structure being far less rigid than others, and is responsible for the movement of certain parts which may not themselves be attached to muscles. This is particularly well illustrated by the functioning of the capsule (Sharif's (1945) 'pumping bulb', see also Rothschild & Traub, 1971, pp. 17-21), in which sperm is deposited on the penis (Fig. 2a) and subsequently squeezed out on to the forked end or spoon-shaped penis rod as it passes forward in front of the opening of the capsule. Both the lunar and satellite sclerites can, owing to the greater flexibility of the untanned portions on either side of it, 'collapse' on to the floor of the capsule, thus obliterating the cavity, which pushes or squirts out the contents like paste pressed out of a tube. A less elaborate mechanism, involving the juxtaposition of tanned and untanned cuticle, ensures the expulsion of sperm from certain types of spermatheca, which is well illustrated in *Spilopsyllus cuniculi* (Dale) (see Fig. 2b). The bulga of the spermatheca consists of tanned, and the hilla of untanned cuticle, except at the tip to which the muscles are attached (Fig. 2b). When these muscles contract, the tip is pulled downwards, and, owing to the flexible nature of the body of the untanned hilla, this bends sharply and acts like the downstroke of a pump handle. Sperm is churned up in the lumen and forced out into the spermathecal duct (which is always composed of untanned cuticle), a few at a time. It is worth noting that the first sperm to enter the spermatheca line the strigillae of the bulga. When the bulga is nearly full, a space funnel is formed, and the sperm which enter thereafter are drawn up through this gap into the hilla. Although the sperm 'first in' now lie nearest the exit, and are best placed to be 'first out', sections show that the pumping action of the untanned hilla mixes up the sperm very thoroughly and it seems the orderly sequence is then lost. It is interesting that at this stage, as in the testis of many fleas (see Rothschild *et al.*, 1970), there is an elaborate mechanism — in the latter case the migration of sperm bundles within the testis — to ensure a mixture of age groups among sperm.

The importance of 'inserts' of untanned cuticle for the movement of the aedeagus and other parts, can only be assessed with the aid of stained sections, but once their importance has been appreciated they can often be 'spotted' in whole mounts since they appear paler than adjacent areas. In the adult flea any area of cuticle which stains pillar-box red indicates that increased flexibility is required in the area and pinpoints some special function (Rothschild & Schlein, 1975).

One other interesting example of movement dependent on the alternation of tanned and untanned cuticle can be mentioned here. Many male fleas possess a feathery, membranous flap at the end of St. VIII, designated the vexillum by Smit (1972), which is used by the male during copulation

for brushing the female pygidium (Holland, 1955) and by systematists as a 'good character'. The male *Archaeopsylla erinacea* (Bouché) has a structure, reminiscent of the vexillum, which is a feathery expansion of the edge of the movable process of the clasper, not of sternum VIII. If a flea is examined alive under a cover-glass in a drop of water, this brush-like organ can be seen to vibrate rapidly with a flickering movement vaguely reminiscent of the mouthparts of a feeding crustacean. Since this fringe is part of the clasper, its independent movement was something of a puzzle until sections revealed that the area adjoining the main body of the clasper is constructed of extremely thin untanned cuticle and acts like a hinge allowing the fringe to flap back and forth at high speed.

In species which live in protected sites, like *Tunga* and to a lesser degree *Ancistropsylla* and *Chaetopsylla* (Rothschild & Schlein, 1975) the tanning of the cuticle is reduced in both degree and extent, and such fleas are a boon to the section cutter. In *Tunga monositus* Barnes & Radovsky, the terminal portions of the tracheae*† are of untanned cuticle and stain bright red, while in *T. caecigena* J. & R. they are mainly pale blue in colour. The degree of sclerotisation and tanning reflects the intensity of host harassment to which fleas are exposed. Thus species infesting rabbits, like *S. cuniculi* and *Cediopsylla simplex* (Baker), which are partially fixed fleas, but, unlike *Tunga,* unprotected by the hosts' skin, are exposed to maximum attack. These lagomorphs not only pull down their ears over their faces and scrape off the fleas attached to the margins, but indulge in extensive mutual grooming (Rothschild & Ford, 1966, 1973). Thus rabbit fleas are among the most highly sclerotised species and are the despair of the section cutter.

Only fleas occupying protected sites can afford the expanded abdomens of gravid females (neosomy, Audy *et al.*, 1972). It should be noted that these greatly enlarged intersegmental membranes consist of arthrodial membrane only, which attains a higher degree of flexibility. Similarly the all important rotation of the link-plates which ensures stiffening of the thorax before take-off (Rothschild & Schlein, 1975), is made possible by an abrupt insertion of arthrodial membrane in the margin of the lateral metanotal area.

It is also of interest that a deep infolding of similar tissue is situated at the base of the pronotal combs†. The precise function of these structures still gives rise to discussion. The most general belief is that the combs merely enable the flea to move smoothly and swiftly through fur, and Humphries (1966) has shown what he believes to be a correlation between pelt density and hair diameter with the distance between individual pronotal spines (see also Traub & Evans, 1967; Smit, 1972). Dr. Jordan, however, told me personally, and Professor Traub arrived independently at the same

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* Many parts of the tracheae in other fleas are virtually colourless or stain very pale pink. The latter shade is well shown in the lozenge shaped expansion of the tracheae in the first tarsal segment, originally described by Furlonge (1872). This author noted that in living fleas it contracts rhythmically. Redescribed by Wigglesworth (1950) it is also illustrated by a photograph in Rothschild *et al.*, (1975).

† Photographs (coloured) of the structures marked thus † in the text can be seen the Natural History Museum (Rothschild Collection of Fleas).

concept — a hypothesis rejected by Mr. Smit — that fleas use the pronotal comb as a movable unit with which they can clamp on to fur. Certainly the large fold of arthrodial membrane below the comb enhances this suggestion, since it ensures greater freedom of up and down movement, whereas rigidity could be expected if it acted only as a conventional comb. But the arrangement of muscles in this area is enigmatical. Dr. Schlein, whose views I sought on this point, since he is well acquainted with the muscles of the flea's thorax (Rothschild & Schlein, 1975), has another and most intriguing suggestion. He thinks the combs are not used for grasping hair, but are essentially devices for the protection of intersegmental arthrodial membrane. Thus the flea with a flexible thorax and capable of sinuous movements, will require longer and more numerous and stouter spines. Thus you would, by and large, expect Ceratophyllid fleas to have more spines in their pronotal combs than Pulicid fleas. The more compact and rigid the thorax the less need would there be for combs. Obviously in a fixed flea like *Echidnophaga* the lack of movement through hair, plus the unusually narrow, rigid thorax associated with their feeding habits, would be factors acting together to eliminate combs. Unfortunately I have never watched cat fleas with this point in mind, but one is struck by their unusually generous endowment of arthrodial membranes between pronotum and thorax, coupled with massive pronotal spines. Have they more sinuous movement than, say, *Xenopsylla cheopis* (Roths.)? Certainly bat fleas like *Ischnopsyllus octactenus* (Kolenati) have supple bodies and sinuous movements, but I have not sufficient sectioned material, or observed enough species alive, to make the necessary comparisons between bat fleas with and without strong combs.

In the pharate adult these areas of cuticle which first take up the distinctive stains are particularly significant, for they usually indicate areas which come under special strains and stresses in the freshly emerged adult. The early staining of the resilin in the pleural arch† is a case in point.

The bursa couplatrix of the bird fleas of the genus *Ceratophyllus* also appears bright red before any other part of the body. Since these fleas frequently pair within seconds of emergence (Holland, 1955; Rothschild & Clay, 1952), presumably before they are fully tanned, and the female organs must take the full impact of the extrusable portion (fistula) of the male aedeagus, this organ requires special protection. The pleural ridge of good jumpers (Rothschild & Schlein, 1975) is often tanned in the pharate adult — an exceptional circumstance.

In cultures of *S. cuniculi* sprayed with chlormadinone and also with cortisol, monstrous malformations of the cuticle occurred quite frequently. The tanned and untanned portions then presented a most bizarre effect (Fig. 5b)* with the layers often reversed, the former (staining yellow) occurring beneath the latter (staining red) and arthrodial membrane (blue) overlaying untanned cuticle.

DIFFERENCES IN SPECIFIC ORGANS

(a) *Central nervous system*

The more compact body of Pulicoid fleas, as we have said, is also reflected in the central nervous system, and the straggling nerve cord of, e.g. a

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* These gross malformations prompted me to warn my daughters most earnestly against the use of the mini pill.

Helmet or bat flea, presents a great contrast with that of *Xenopsylla* and its allies. A most drastic modification in the ventral nerve cord of the male is found in *Tunga monositus* and probably in related species. In the early pharate pupa (Fig. 3a) this occupies a normal position similar to that of the female. During development the terminal portion shifts dorsad, so that it forms a V-shape and eventually the terminal ganglion comes to lie in the dorsum — thus making space for the developing massive aedeagus (Fig. 3b). The shift is not purely mechanical since in the developing pupa it precedes the development of the aedeagus. There is little doubt that a closer study will reveal further modifications of the central nervous system. The most disappointing aspect of the flea's brain is its poor staining quality and the difficulty this presents in studying neuro-secretion.

(b) *Salivary glands*†

In all fleas these consist of simple paired elliptical or pear-shaped glands with a central salivary reservoir. Each gland leads into a duct which unites to form a single main duct on each side of the body. These superficially resemble tracheae since they are almost colourless in stained material and 'ringed'. In *Chaetopsylla* the ducts are long and surprisingly very slender, while in *Echidnophaga* they are stout with conspicuous bulging cells in the epithelial covering. Like the ovaries and midgut epithelium the salivary glands undergo cyclical development during sexual maturation. The secretory cells themselves enlarge enormously and a dramatic change may occur in the staining properties of the secretion seeping from them into the lumen. Even where these changes are allowed for, it will be seen that there are subtle specific differences in all salivary glands. Broadly speaking, in Hystrichopsyllids they are relatively large, whereas in bat and bird fleas they are small. In *Xenopsylla cheopis* there are 8-12 cells per gland, but in the semi-sedentary female rabbit flea, *S. cuniculi,* each consists of about 14-24 cells (Rothschild *et al.,* 1970, p. 119), while in female *Tunga* a large part of the thorax is filled with relatively enormous ramifying salivary glands. It therefore comes as a surprise to find that in *Echidnophaga gallinacea* (Westwood) which is nearer in habit to *Tunga* than *Spilopsyllus,* the gland is the smallest yet recorded, and each consists of only four cells. *Stenoponia* has very distinctive glands with a densely packed lumen with a specialised valve† at the exit and even in gravid females the secretion does not take up any colour when treated with Mallory's triple stain. Whether this type of gland is characteristic of the whole subfamily has yet to be seen.

(c) *The midgut*†

Apart from *Tunga monositus* and an undescribed sibling species in Traub's collection, all known fleas possess proventricular spines. However, in view of the obvious differences in the number, size and shape and the sexual dimorphism of these structures (Deoras & Joshi, 1958; personal observations), it is to be expected that, despite the basically uniform nature of the flea's diet, the contents of the midgut present marked differences in sectioned material. It has been demonstrated that the gut lining also undergoes a cyclical change associated with maturation (Rothschild *et al.,* 1970). Nevertheless it is surprising that in two species of Pulicoid fleas, such as the rabbit and European hedgehog flea, which are both host specific and essentially 'body' fleas, spending only a minimal period away from the host in the nest, the gut contents are so characteristic of each species. In the fully matured egg-laying female hedgehog flea it is dark chocolate brown in colour with slate grey/black fleckings, often showing a bolus or several

rounded conglomerations, the whole mass consisting of extremely fine particles. In the egg-laying rabbit flea the gut content usually stains bright red and whole blood cells (Rothschild *et al.*, 1970) are conspicuous and passing rapidly through the gut at this stage. An even greater contrast is presented by certain Leptopsyllid fleas (e.g. *Stigmactenus toxopeusi* Smit) in which the contents stain a uniform pale sky-blue colour.

In the two Pulicoid fleas mentioned above, the mid-gut epithelium of the gravid female is esentially of the same type (Fig. 4a) with closely packed single finger-like columnar cells (about 4,000 in the rabbit flea, Rothschild *et al.*, 1970) contrasting sharply with that of the egg-laying *Hystrichopsylla talpae* (Curtis) in which the epithelium is organised into more definite 'villi', each composed of several groups of cells, with species between the 'villi' (Fig. 4b). This condition has only hitherto been found in the Hystrichopsyllidae, and is less conspicuous in *Ctenophthalmus* than in *Hystrichopsylla* and *Stenoponia*. In fleas like *X. cheopis* and *Nosopsyllus fasciatus* (Bosc.) with an extended period of egg-laying, the epithelial cells are not so densely packed as in the rabbit and hedgehog fleas, but grouped (bunched at the base) with spaces between them. In fleas which only occupy the host's breeding stop and nest for limited periods, a large number of eggs must ripen simultaneously (egg-laying lasts only about 10-20 days in *S. cuniculi*) and they consequently require a period of intense feeding and rapid digestion. Darskaya (1964) has also pointed out the contrast in rates of digestion in different types of bird fleas. So far, however, the enzymes involved have not been compared: no doubt, like the secretion of the salivary glands, they will reveal some interesting specialisations.

(d) *Ovaries and secretions of the oviducts*

An important distinction characterises the ovaries of the Hystrichopsyllids, although it is not equally evident in all genera or even species. In *Stenoponia* the ovaries are pseudo- or secondarily polytrophic, not simple panoistic ovaries like those found in the rest of the order (Kunitskaya, 1960; Hopkins & Rothschild, 1966, Vol. IV, Plate 12B). The oocytes are separated by groups of 'nurse cells' with a duct leading from them to the developing oocytes. In *Hystrichopsylla* and *Ctenophthalmus* a well defined duct has not been found and the nurse cells are less well developed or rudimentary.

In the rabbit flea the lateral ovarioles (six a side) are unbranched, but in other Pulicoid fleas such as *X. cheopis* there is branching of these structures†, and simultaneous ripening is limited to the proximal oocytes. Such modifications seem to occur sporadically throughout the order and like the loss of the pleural arch, may merely be linked to specialised habits, possibly, as in this case, to an extended breeding season, or a long occupation of burrows in the company of both young and adult hosts.

The secretion of the extrachorion material (by the epithelial lining of the terminal portion of the ovarioles, the lateral and common oviducts, Rothschild & Ford, 1965) is astonishingly varied, both in texture and staining properties, through the order. This is presumably dependent on the requirements of the developing eggs and the site of oviposition. In the Hystrichopsyllids so far examined (see Table 1) the main basic secretion of extrachorion material stains bright scarlet. In *Stenoponia* the two huge eggs are incased in a cement-like covering (an adaptation to sandy and desert-like conditions, and possibly also a protection against mites?) and large golden staining globules† (fat globules?) float in the scarlet fluid. In *Hystrichopsylla* a thinner blue staining secretion, only discernible at the extreme distal end of the oviduct, mixes with the red globules in the vagina.

I confess I have not identified the cells in the oviducts also secreting the blue staining element in the extrachorion material either in this species or in *X. cheopis* and *S. cuniculi*. Like in the case of the salivary gland secretion, it is probably produced by the same cells under different hormone control.

In most fleas the common oviduct, although rather short, extends some distance beyond the junction with the lateral oviducts (which receive the ovarioles) but in *Hystrichopsylla* it is exceptionally short, and, as we have stated previously, the vagina is long and divided into a distal (posterior) and proximal (anterior) portion separated by a clamp (Rothschild, 1965; Rothschild & Traub, 1971, Plate 6B), the latter lined with tall epithelial cells. This terminology is somewhat arbitrary since I have been unable to decide from the pupal material at my disposal whether the 'common oviduct' is of endodermal or ectodermal origins, or both. In *Stenoponia* the whole canal from clamp to ovarioles is homogeneous and secretes extrachorion material throughout and would be unhesitatingly described as a very long common oviduct. The same applies to *Ctenophthalmus* where the clamp is not developed. Put in *Polygenis*. for example, and in an undescribed species in Colonel Traub's collection, the first portion of the canal beyond the clamp is cuticle-lined and would in these cases be equally confidently described as 'vagina'. Clearly this point cannot be decided without the examination of further material, especially the pupal stages. It should also be noted that the clamp can vary in position, sometimes situated in the floor and at other times in the roof of the canal. It is probably a very important structure, checking the eggs in front of the opening of the bursa during their passage along the main canal—thus ensuring fertilisation.

The common oviduct of *Tunga* (in the four species examined) is provided with immensely fine, cilia-like extensions of the lining†, which in addition to the muscles attached to the vagina in these species, presumably assists the passage of eggs to the exterior. Oviposition probably presents special difficulties for the endoparasitic species, for the eggs could well remain entangled round the orifice, which barely protrudes above the surface of the host's skin.

(e) *Male organs*

During the maturation in the male flea the spermatazoa in the testis undergo a series of dramatic changes which are similar in most, but by no means in all fleas, and concern their organisation into migrating bundles (Rothschild *et al.*, 1970) and then the breakdown of such bundles and the passage of individual sperm out of the testis into the epididymis and the paired vas deferens and thence into the ejaculatory bulb. However, in *Rhopalopsyllus* the bundles are rather loosely formed, apparently all at the same stage of development, and members of this genus have apparently dispensed with migration of spermatozoa within the testis.

During this progress of maturation the sperm pass through a stage where they beat synchronously within each bundle (Fig. 5)*, the frequency of the waves altering according to the stage of development (Rothschild *et al.*, 1970). While allowing for these cyclical changes it is nevertheless obvious that the 'waving' of the sperm within the testis differs markedly from species to species, just as the number of bundles varies as well as the

* This photograph was originally submitted for publication with the caption 'Advert. for mermaids' hair tonic?' but one of the referees considered it too frivolous.

length of individual sperm. The Echidnophaginae have exceptionally long sperm which is correlated with an unusually large spermatheca — despite the comparatively small size of these fleas.

Histologically the two pairs of accessory glands† are distinctive and presumably each provides specialised secretions, but in the majority of fleas examined they respond negatively to the staining techniques used (*Polygenis* is an exception). Nothing is known about these structures and they present virtually an untouched field awaiting further investigation both with regard to their form and specific function.

The ejaculatory bulb would also repay further study. In *Hystrichopsylla talpae* (Curtis) the cuticular lamellae† are more deveoped than in most fleas. In *Polygenis* the bulb† is much broader and larger altogether, in comparison with the aedeagus, and the lamellae are very poorly developed or absent. Possibly there is some connection between this type of bulb and the simultaneous ripening of all sperm bundles.

(f) *The rectal ampulla and rectal pads*

In the pharate adult the hind gut runs uninterruptedly from the opening of the midgut to the anus (Fig. 7a). This is still evident while the cuticle-lined rectal ampulla (which has, among other functions, the specialised role of providing the larvae with blood meals) is developing and already surrounds it (Fig. 7b). In the adult flea that part of the gut which traverses the rectal ampulla completely disappears and the hind gut enters it at the proximal end.

In Hystrichopsyllids the rectal pads are highly developed and the cuticular spines on the surface much in evidence (see also Fig. 6b). There is a deeply folded blue-staining lining to the ampulla and the whole organ is muscular, especially in *Stenoponia*. In species which tend to fix to the host, such as *Chaetopsylla*, the rectal pads are poorly developed. There are only two instead of the usual six in *Echidnophaga* (except in three African species in which, Mr. Smit tells me, there is the usual complement) and in *Tunga* but they are most degenerate in the latter. Furthermore in *T. monositus* (and Traub's undescribed species) an extraordinary modification occurs, no doubt associated with the fact that the larva does not feed (Barnes & Radovsky, 1969) and therefore the function of the ampulla as purveyor of blood meals has lapsed. The innermost layer is replaced by a lining of giant epithelial cells with the comparatively tiny rectal pads perched on the surface (Fig. 6a). The development of giant cells (possibly with polytene nuclei) throughout the body of *T. monositus* (this 'gigantism' involves the fat body, body wall, oenocytes, etc.) is, in the author's opinion, of sufficient significance (together with other characters such as the spineless proventriculus) to justify the erection of a separate genus for this species and the undescribed sibling species in Traub's collection. In the related *T. caecigena* no giant cells are developed, but a similar tendency can be seen in *T. penetrans* (L.) (but not in the ampulla).

(g) *The fat body*

Since the fat body†, like the midgut and sperm bundles, undergoes cyclical development linked to maturation, the same caution must apply to the interpretation of the variations found in this organ. But providing similar stages are compared, derived from the same area of the body, it will at once be appreciated that there are many variations in the fat body of different species. Two extreme types are illustrated by gravid specimens of *H. talpae* and *Polygenis klagesi* J. & R.: the former have a heavily

staining nucleus, a feature which is conspicuously absent in the latter (see Plate 6B in Rothschild & Traub, 1971).

(h) *Muscles*

Anyone examining longitudinal sections of a series of different species of fleas is instantly struck by the densely packed muscle fibres in the thorax of one species and the relative paucity in others. In some cases, for example in *Echidnophaga,* this lack of muscles is easily correlated with a relatively sedentary life, and resorbtion of muscles seems to occur after fixation to the host, but our ignorance of the habits of most fleas is such that we can rarely make any sense of what we see. Similarly the fibrils are far more widely spaced in some species than in others. During our study of the jumping muscles of *X. cheopis* (Rothschild & Schlein, 1975) we noted that '63B' was lacking in all Pulicoid fleas — a peculiarity of the family. I also noticed in passing that certain bat fleas possessed a tergo-pleural muscle which appeared to be lacking in other fleas, and this may also prove to be a family character. Finally the muscles of *Tunga* are highly specialised, with thread-like fibres, unlike any other adult flea yet studied, and, superficially at any rate, reminiscent of larval muscle. In *T. monositus* the oviduct is highly muscular and the eggs must be forcibly expelled at oviposition. This was anticipated by Jordan (1962), who noticed that the bristles round the external opening of the oviduct in the endoparasitic *T. caecigena* were so arranged as to assist in the violent expulsion of the eggs.

Finally muscles do not all show the same affinity for stains in the different families of fleas. Making due allowances for the variation in fixing the processing, on the whole the muscles of the Pulicoid fleas show an affinity for analine blue which is lacking in those Ceratophyllid fleas examined up to date.

DISCUSSION

When assessing the internal organs of the flea as an aid to classification and the clarification of phylogeny, one is again confronted with Jordan's central problem: the characters concerned may provide basic information about the higher categories and phylogeny — like for instance the presence of the pleural arch — but also simultaneously reflect parallel adaptations occurring sporadically throughout the order in response to the life-style of both parasite and their different hosts. What becomes clear, however, is that distinguishing characters of the soft parts of fleas, if selected wisely, can add materially to the combination of significant external characters which are employed in the description of families, genera and species.

Despite the flea's adaptation to a parasitic life-style, loss of wings, development of unique saltatorial powers and the modifications to the exoskeleton associated with life in fur and feathers, broadly speaking its internal organs, are simple and stereotyped. Moreover, because of the evolutionary straight-jacket in which the order seems to be encased, the ground plan is uncomplicated and basically similar. This simplifies description but also gives full and clear expression to the plethora of small differences which never cease to astonish and delight the comparative morphologist, and a combination of which, selected by a Karl Jordan, can throw light on higher classifications. Furthermore, section at 8 μm, a single specimen can usually be accommodate on one slide. These considerations taken together confirm the flea as an excellent subject for a brief insect histology, which is badly needed both for teaching purposes and for use in conjunction with bacteriological and viral studies.

It is often said that morphology is dull. But this is of course totally untrue, although nowadays we are ashamed to admit how fascinating we find the comparison between the backsides of insects. In studying the soft parts of fleas one is captivated by the *apparently* nonsensical variations which one assumes must be adaptive. Why do males require fewer proventricular spines than female fleas? There must be some sort of link between the loss of proventricular spines in *Tunga,* their sessile life-style, and their large salivary glands, not to mention the bunch of glands at the entrance to the midgut which stain up so well in this genus. But why then should *Echidnophaga,* also a fixed flea with apparently a rather similar life-style, have *more* and larger proventricular spines than usual, and small salivary glands? Humphries (1966) suggested a meaningful link between hair and the gaps between comb teeth. How about the size of blood cells one so often sees caught in the gaps between proventricular spines? Is there some link between the morphology of mammalian blood and the plethora of minor variation in the spines? Or do these in some way reflect the need in certain species for fast and infrequent meals, or in others more or less continuous feeding? And what relation, if any, is there between the rapid and slow digestion types noted by Darskaya (1964) and the variation in the epithelial cells in the midgut and the quality of the midgut content? The mind boggles at these conundrums. It was obviously a sad error in evolutionary planning that entomologists have been endowed with only one life. I recall Dr. Jordan, aged 95, stone deaf, assisted by a curious pin-hole eye-piece (which he claimed concentrated the light in his microscope), puzzling ecstatically over the eccentric pronotal comb of *Barreropsylla* which he was in the process of describing (Jordan, 1953), shouting cheerfully: 'In the next world I will know all the answers.'

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MIGRATORY MOVEMENT OF THE BROWN-VEINED WHITE (BELENOIS AUROTA F.)

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On 25th November 1975, at Vom, near Jos, Plateau State, Nigeria, a flight of white butterflies was noted.

The butterflies were moving towards the South-East at a height of 1 m to 3 m above the ground. They were counted for ten minutes over a 50 m front, and 500 passed in this time. The movement was checked over a distance of one kilometre, the movement being continuous over this distance. It continued for at least four hours. The weather was hot and sunny, with a very few small clouds. Wind was of force 3 to 4 at first, increasing to 4 to 6 later, coming from E. or E.S.E. all the time.

From closely-observed and captured specimens, the species was determined to be *Belenois aurota* Fab., the Brown-veined White. The flight appeared to be very determined, though a very few insects hesitated over a patch of garden flowers. No other species was noted in the flight at any time, though other species were present in the area. The estimated rate was 60,000 per one-kilometre front per hour. The table gives details of the daily rates for the period concerned.

Place	*Date*	*Number counted for 10 min over 50 m front*	*Calculated number on 1 km front per hour to nearest 1,000*
Vom	Nov. 25	500	60,000
Vom	Nov. 26	90	11,000
Vom	Nov. 27	150	18,000
Vom	Nov. 28	70	8,000
—	Nov. 29	No observations	—
Miango	Nov. 30	270	32,000
Vom	Dec. 1	1,000	120,000
Vom	Dec. 2	1,000	120,000
Vom	Dec. 3	200	24,000
Vom	Dec. 4	200	24,000
Vom	Dec. 5	A few	—
Vom	Dec. 6	Very few	—

Fig. 1